

DESMID ZYGOSPORES FROM FRENCH GUIANA AND THE PHENOMENON OF SIMULTANEOUS CONJUGATION IN MULTI-SPECIES ASSEMBLIES

P.F.M. COESEL

Department of Aquatic Ecology, University of Amsterdam,
Kruislaan 320, NL — 1098 SM Amsterdam

ABSTRACT — Sexual reproduction stages of fifteen desmid taxa were encountered in a tycho plankton sample from a shallow rain-forest pool in French Guiana. Zygosporae are depicted for nine taxa. Those of *Cosmarium dimaziforme* (Grönbl.) A.M. Scott et Grönbl., *Euastrum ciastonii* var. *apertisinuatum* Scott et Prescott, *Groenbladia bourrellyi* stat. et nom. nov. (synonymous to *Hyalotheca neglecta* var. *major* Taylor), *Staurastrum eskolense* nom. nov. et stat. nov. (synonymous to *S. elegantissimum* var. *brasiliense* Förster) and *Xanthidium trilobum* Nordst. are new to science. The phenomenon of simultaneous conjugation by a number of different desmid taxa, also known from literature, might be explained by the production of non-species-specific pheromones inducing mating activity in a number of related algal species.

RÉSUMÉ — Les stades de reproduction sexuée de quinze desmidiées ont été observés dans un échantillon de tychoplancton provenant d'une mare peu profonde de la forêt tropicale humide de Guyane française. Des zygosporae ont été figurées chez neuf de ces taxons. Ceux de *Cosmarium dimaziforme* (Grönbl.) A.M. Scott et Grönbl., *Euastrum ciastonii* var. *apertisinuatum* Scott et Prescott, *Groenbladia bourrellyi* stat. et nom. nov. (synonyme de *Hyalotheca neglecta* var. *major* Taylor), *Staurastrum eskolense* nom. nov. et stat. nov. (synonyme de *S. elegantissimum* var. *brasiliense* Förster) et *Xanthidium trilobum* Nordst. sont nouveaux pour la science. Le phénomène de conjugaison simultanée d'un bon nombre de desmidiées, connu aussi dans la littérature, pourrait être expliqué par la production de phéromones non spécifiques au niveau de l'espèce, induisant l'activité d'accouplement chez un certain nombre d'algues apparentées. (Traduit par la Rédaction)

KEYWORDS: desmids, freshwater algae, zygosporae, conjugation, pheromones, French Guiana

INTRODUCTION, MATERIAL AND METHODS

In February 1995, a number of freshwater habitats in northeastern French Guiana were sampled and searched for desmids. One small, rather shallow pool with ochreous-coloured water, near the settlement of Eskol, just north of the road from Roura (ca 20 km south of Cayenne) appeared to be remarkably rich in desmid zygosporae. The

pool was partly filled in with *Utricularia* (presumably *U. myriocista* St. Hil. et Girard), which served as the substrate for the algae sampled. To this end, *Utricularia* material was squeezed out. In the thus obtained samples also electric conductivity was determined, using a portable WTW-LF92. Conductivity of the sample containing the zygospores described below measured $51 \mu\text{S cm}^{-1}$. Shortly after collecting, the samples were fixed with formaldehyde to a final concentration of about 4%. Algal material was studied light microscopically (Wild M20) and drawings were made with the aid of a drawing tube. The sample containing the below-described zygospores is admitted into the algal collection of the Amsterdam Herbarium, under no. 95.05.

OBSERVATIONS

Cosmarium dimaziforme (Grönbl.) A.M. Scott et Grönbl.
var. *concavum* Förster ex Förster (Figs 5-8)

Cosmarium dimaziforme, a species with a predominantly Latin American distribution (e.g. Förster, 1982; Thérèzien, 1985), includes several, closely related varieties, all known only in the vegetative state. In the Eskol sample, zygospores of var. *concavum* (Förster, 1982) were encountered. The spores were globular and ornamented with rather short spines arising from a conical base (Figs 7-8). Zygospores, including spines were 23-35 μm in diameter.

Euastrum ciastonii Racib.
var. *apertisinuatum* Scott et Prescott (Figs 1-4)

Euastrum ciastonii, known from North and South America (Krieger, 1937), has only been recorded once in a sexual state (Prescott & Scott, 1945, t. 8: 9). The accompanying figure is rather schematic, showing a globular, spiny spore with a single semicell next to it. To date, var. *apertisinuatum*, differing from the nominal variety by a widely opened sinus, was only known in vegetative state. In the Eskol sample, zygospores 42-50 μm in diameter were encountered. The shape accords with that of the nominal variety.

Groenbladia neglecta (Racib.) Teiling (Figs 9-12)

In our Eskol sample, two species of *Groenbladia* were present. Specimens of the most common one, depicted in Fig. 9, are in good agreement with *G. neglecta* as originally described by Raciborski (1895). According to his diagnosis, *G. neglecta* is characterized by more or less barrel-shaped semicells, showing 6-8 transverse rows of marked cell wall pores. Zygospores of *G. neglecta* were recorded by West & West (1898, under the name of *Hyalotheca neglecta* Racib.) from England, by Scott & Grönblad (1957, concerning var. *elongata* Scott et Grönbl.) from the southeastern United States, and by Grönblad *et al.* (1968, also referring to var. *elongata*) from tropical West Africa. Whereas West & West (*loc. cit.*) described the zygospores of *G. neglecta* as rounded and smooth-walled, zygospores of its var. *elongata* were found to be quadrangular with slightly retuse to straight sides.

Zygospores (Figs 10-12) belonging to *G. neglecta* cells answering Raciborski's diagnosis were abundant in the Eskol sample. They were more or less globular and smooth-walled and resembled those figured by West & West (*loc. cit.*), their dimensions — ca 20 to 30 μm in diameter — are comparable.

Groenbladia bourrellyi stat. et nom. nov. (Figs 13-15)

Replaced synonym: *Hyalotheca neglecta* var. *major* Taylor 1935, p. 222, t. 49: 14.

The second species of *Groenbladia* differs from *G. neglecta* in a number of features. Semicells are cylindrical with their greatest width at the base rather than in the midst (so chimney-pot-shaped rather than barrel-shaped; Fig. 13). The cell wall is somewhat thicker than in *G. neglecta* and does not show the transverse rows of pores. Pores, if distinguishable at all, are not arranged in a particular pattern. Zygospores are angular (Figs 14-15) versus rounded in *G. neglecta*. Screening of literature shows that this taxon has been recorded under *G. neglecta* (or *Hyalotheca neglecta*), usually without particular comment (e.g. Grönblad, 1921; Scott *et al.*, 1965; Bourrelly, 1966) and sometimes by indicating it as a "forma" or separate variety. Bourrelly (1957, p. 1094) distinguished two different forms within Sudanese material of *G. neglecta*. Whereas his "forma 1" could be identified as "true" *G. neglecta*, his "forma 2" is in good agreement with our cylindrically-shaped cell material. That taxon also was reported by Bourrelly (1961, p. 351, t. 24: 4) from Ivory Coast, also as "forma". However, much earlier, Taylor (1935, p. 222, t. 49: 18) had already described *G. neglecta* var. *major*, the diagnosis of which perfectly fits the characteristics of the alga shown in Fig. 13. As it differs from "typical" *G. neglecta* not only in cell shape, but also in cell wall sculpture and zygospore morphology, I prefer to distinguish it at species level. By naming it after Pierre Bourrelly, both Bourrelly's contribution to the taxonomy of this species and his significance to desmidiology in general are expressed. In the Eskol sample investigated, zygospores of *G. bourrellyi* were common and measured 28-36 µm in greatest length.

In view of the above-discussed characteristics of *G. bourrellyi*, *G. neglecta* var. *elongata* Scott *et* Grönbl. is transferred to this species:

G. bourrellyi var. *elongata* (Scott *et* Grönbl.) comb. nov.

Basionym: *G. neglecta* var. *elongata* Scott *et* Grönbl. 1957, p. 48, t. 35: 17-24.

Penium exiguum W. West (Figs 28-30)

As far as known, this cosmopolitan species was only once recorded with zygospores, i.e. from The Netherlands, by Beijerinck (1926, p. 50, t. 9: 191). The (irregular) globular zygospores (Figs 29-30) commonly occurring in the Eskol sample agree with Beijerinck's report both in morphology and diameter (17-24 µm).

Staurostrum eskolense nom. nov. et stat. nov. (Figs 16-22)

Replaced synonym: *S. elegantissimum* Johnson var. *brasiliense* Förster 1969, p. 81, t. 46: 1-3.

The alga depicted in Figs 16-20 is in good agreement with *S. elegantissimum* var. *brasiliense* as described by Förster (1969) from the Amazon area and later on also recorded from French Guiana (Thérézien, 1985, p. 132, t. 39: 8). However, the taxon in question is distinctly different from *S. elegantissimum* as originally described by Johnson (1894, p. 290, t. 211: 16). Our entity is characterized by a cup-shaped semicell body, with an interrupted, annular series of spines and granules at its base. The spines alternate in position with radiating processes. A variable number of smaller, acute granules occur next to these spines (Figs 19-20). In contrast to that, *S. elegantissimum* as figured by Johnson (*loc. cit.*) and, e.g., Scott & Grönblad (1957) is marked by a cylindric semicell body, ornamented with a regular, supraisthmial series of equally sized spinelets. In this feature, *S. elegantissimum* shows relationship with *S. johnsonii* W. *et* G.S. West, and *S. pseudosebaldi* Wille. Therefore, I prefer to classify var. *brasiliense* as a separate species. As the names

of *S. brasiliense* Nordst. and *S. foersteri* Coesel already exist, the species is named after the locality where it was found, i.e. Eskol.

S. eskolense was frequently met with in a sexual state. Zygospores were globular and furnished with long, apically furcated spines. Including spines, zygospores were 60 to 70 μm in diameter (Figs 21-22).

Xanthidium trilobum Nordst. (Figs 23-27)

To date, this species, characterized by a Latin American distribution (Coesel, 1996), was only known in vegetative state. Zygospores in the Eskol sample (Figs 26-27) were globular in shape and provided with rather long, apically furcated spines. Spores were 85-110 μm in diameter, including spines.

Unknown zygospore, type I (Figs 31-32)

According to the shape of both spores and adhering empty cell parts, as well as the absence of any visible somatic cell wall sculpturing, the algal form figured presumably belongs to the Fam. Mesotaeniaceae. However, since chloroplast morphology in the formaldehyde-fixed sample could not be studied it is an open question whether it concerns, e.g., a *Cylindrocystis* or a *Mesotaenium* species.

Unknown zygospore, type II (Figs 33-34)

The identity of this algal form is even more questionable than that of type I. The shape of the zygospore reminds that of *Closterium navicula* (Bréb.) Lütkem., but the apices of the adhering cell parts seem too broadly rounded to justify classification under that species (cf. Ruzicka, 1977). Also some *Actinotaenium* species should be considered, e.g., *A. minutissimum* (Nordst.) Teil., and *A. mooreanum* (Arch.) Teil. (cf. Ruzicka, 1981).

DISCUSSION

Next to the above-described desmid zygospores and that of the separately discussed *Mateola curvata* (Nordst.) Coes. (Coesel, 1997) some additional spores were found, obviously belonging to desmid taxa but poorly developed or secondarily deformed. Altogether, zygospores of fifteen desmid taxa were found. Remarkably, many other samples collected in the same period and in the same region (some of which were very close to the Eskol site) did not yield any zygospores. This phenomenon of simultaneous multi-species conjugation in desmids has been reported previously (e.g. Beijerinck, 1926; Homfeld, 1929; Coesel, 1974) but, so far, cannot be explained in a satisfying way. No doubt, conjugation is initiated by certain environmental parameters. For instance, it is well-known that mating in *Closterium* is stimulated by nitrogen depletion of the surrounding medium (e.g. Ichimura & Kasai, 1990). As zygospore formation in desmids is a way to survive dry environmental conditions for a shorter or longer periods, one might predict enhancement of conjugation activity in very shallow, drying-up water bodies. However, such conditions do not offer any guarantee of zygospore formation (e.g. Homfeld, 1929), and thus, environmental conditions alone do not trigger the induction of mating behaviour.

There is ample evidence that sexual reproduction in algae, like in other organisms, is under strict control of hormonal processes which, in turn, are regulated by genetically determined sex type and compatibility factors (Van den Ende, 1976). Often, complex hormonal interactions are needed before gametic fusion may be completed. Many pheromones appear to be highly specific, and thus only functional within lower taxonomic units. For the desmid *Closterium peracerosum*, certain pheromones were even shown to be strain-specific (Nojiri *et al.*, 1995; Sekimoto *et al.*, 1995). However, not all sex pheromones are that specific. In the fungal order Mucorales (Zygomycetes) non-species-specific trisporic acids are produced, inducing the formation of sexual structures in a variety of taxa. For instance, trisporic acids secreted by *Mucor mucedo* strongly stimulate zygospore production in *Mucor genevensis*, *Syzigites megalocarpus* and *Zygorhynchus moelleri* too (Van den Ende, 1978). Ectocarpene, a pheromone secreted by the brown alga *Ectocarpus siliculosus*, proved to be the progenitor of a whole series of C₁₁ hydrocarbons which are involved as signals in the sexual reproduction of brown algae (Boland, 1995). Interestingly, the same compounds have also been found among the volatiles released during a phytoplankton bloom in a freshwater lake (Jüttner & Wurster, 1984).

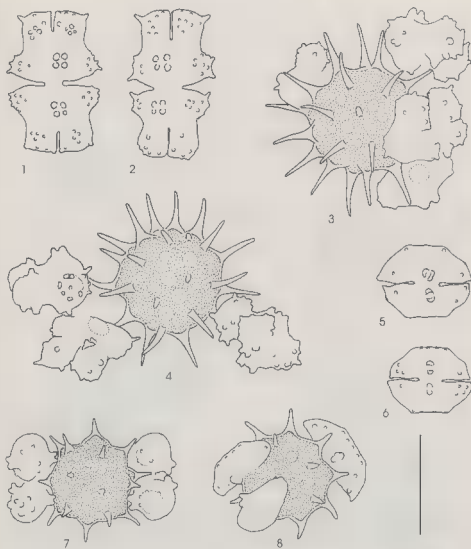
Considering the above, it might be possible that under favourable environmental conditions certain desmid species known for their ready development of sexual stages, e.g. *Cylindrocapsa brebissonii*, produce a non-species-specific pheromone that stimulates other, more or less related species to mating activity. Even a response by desmid species to pheromones produced by non-desmid charophycean algae is possible. In this way the phenomenon of simultaneous conjugation in multi-species desmid assemblies could be explained.

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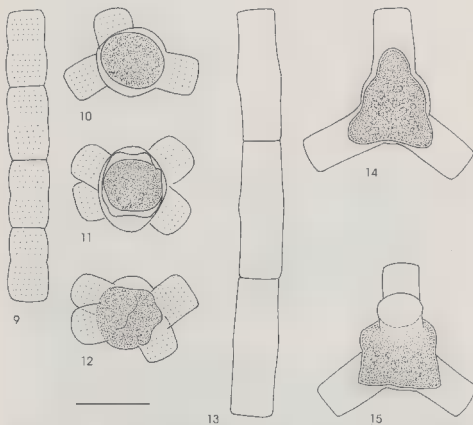
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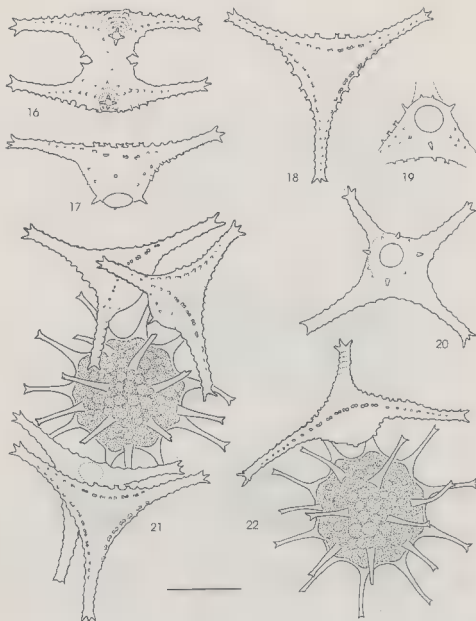
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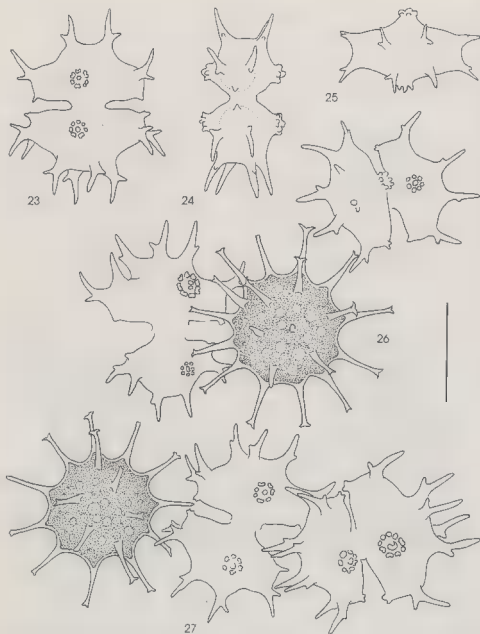
Figs 1-8. Figs 1-4. *Euastrum ciastonii* var. *apertisinuatum*. Figs 1-2. Somatic cells. Figs 3-4. Zygospores with adhering empty gametangial cells. Figs 5-8. *Cosmarium dimaziforme* var. *concavum*. Figs 5-6. Somatic cells. Figs 7-8. Zygospores with adhering empty gametangial cells. Scale bar = 25 μ m.



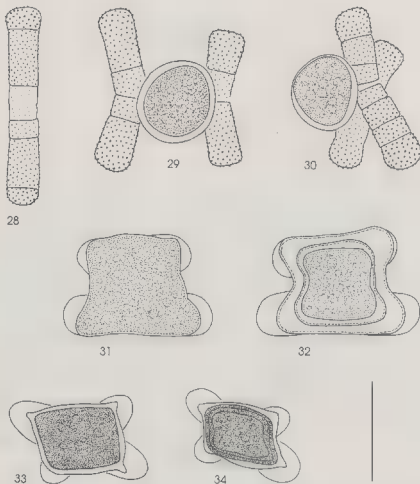
Figs 9-15. Figs 9-12, *Groenbladia neglecta*. Fig. 9. Filament of somatic cells. Figs 10-12. Zygospores with adhering empty gametangial cells. Figs 13-15. *Groenbladia bourrellyi*. Fig. 13. Filament of somatic cells. Figs 14-15. Zygospores with adhering empty gametangial cells. Scale bar = 25 μ m.



Figs 16-22. *Staurastrum eskolense*. Figs 16-20. Somatic cell/semicell in frontal view (16), back view (17), apical view (18) and isthmal view (19-20). Figs 21-22. Zygospores with adhering empty gametangial cells. (Figs 16-19, 21-22: triradiate form; Fig. 20: quadriradiate form). Scale bar = 25 μ m.



Figs 23-27. *Xanthidium trilobum*. Figs 23-25. Somatic cell in frontal, lateral and apical view, respectively. Figs 26-27. Zygospores with adhering empty gametangial cells. Scale bar = 50 μ m.



Figs 28-34. Figs 28-30. *Penium exiguum*. Fig. 28. Somatic cell. Figs 29-30. Zygospores with adhering empty gametangial cells. Figs 31-32. Unknown zygospore, type I. Figs 33-34. Unknown zygospore, type II. Scale bar = 25 μ m.